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INSIGHTS INTO THE SPECIES DELINEATION AND POPULATION STRUCTURE OF *SOLIDAGO SHORTII* (ASTERACEAE) THROUGH MORPHOMETRIC ANALYSIS

JAMES B. BECK

Department of Biological Sciences, 521 Lancaster Ave.,
Eastern Kentucky University, Richmond, KY 40475-3140
Current Address: Department of Biology, Washington University,
St. Louis, MO 63109

ROBERT F. C. NACZI

Department of Biological Sciences, Nunn Drive,
Northern Kentucky University, Highland Heights, KY 41099-0400

PATRICK J. CALIE[1]

Department of Biological Sciences, 521 Lancaster Ave.,
Eastern Kentucky University, Richmond, KY 40475-3140
e-mail: biocalie@acs.eku.edu
[1]corresponding author

ABSTRACT. Short's goldenrod, *Solidago shortii* (Asteraceae), is extant from a single locality in Blue Licks, Kentucky. Field studies demonstrated that this endemic is a morphologically variable taxon, inspiring two questions. First, is the taxon known as *S. shortii* from Blue Licks the same species as originally described by Torrey and Gray from an extirpated population at the Falls of the Ohio River, Kentucky? Second, what is the extent of the morphological variation within and among populations of Short's goldenrod at Blue Licks? These questions were addressed through Principal Components Analysis (PCA), Discriminant Function Analysis (DFA), and standard whole-plant herbarium specimen comparisons. Whole-plant comparisons with other members of *Solidago* subsection *Triplinervae* revealed diagnostic characters suitable for the delineation of *S. shortii*. All specimens of *S. shortii* from both the Blue Licks and Falls of the Ohio localities shared diagnostic character states. For morphometric purposes, specimens representing two sympatric goldenrod species (*S. ulmifolia* and *S. nemoralis*) and one close phylogenetic relative (*S. canadensis* var. *scabra*) were sampled from the same locality as *S. shortii*. Vegetative and floral characters were analyzed for all four taxa. Specimens of *S. shortii* from the Blue Licks vicinity formed a continuous cluster in PCA with specimens from the Falls of the Ohio, a cluster which was distinct from those formed by the other three species. In DFA, the Falls of the Ohio specimens were imbedded in the cluster formed by the Blue Licks specimens. Thus, the taxon at Blue Licks is indeed *S. shortii*, as established by morphometric analysis and whole-plant comparisons. In terms of interspecific variation, *S. shortii* at Blue Licks exhibited a similar or greater range of variation than either of the two more common *Solidago* taxa found at Blue Licks, *S. canadensis* var. *scabra* and *S. nemoralis*. The range of

morphological variation exhibited by *S. ulmifolia* was slightly greater than that of *S. shortii*. These data also indicate a greater variability within and among Blue Licks populations of *S. shortii* than otherwise might be expected for a species of highly restricted distribution, and have major implications regarding management policies.

Key Words: intraspecific variation, morphometrics, species boundaries, *Solidago*, endangered species

There are 295 vascular plant species native to Kentucky (approximately 9.8% of the native flora) that are considered in danger of extinction (Endangered, Threatened, and Special Concern Plants and Animals of Kentucky, Kentucky Nature Preserves Commission, October 1992). One of the more unique species is Short's goldenrod, *Solidago shortii* Torr. & A. Gray, a member of the sunflower family (Asteraceae) and an entry on the Federal endangered species list [Federal Register Vol. 50(172): 36085–36089, 5 Sep 1985]. This species was first described by John Torrey and Asa Gray (1842) from a collection made by Dr. C. W. Short of Louisville from the Falls of the Ohio River in Jefferson County, Kentucky (Braun 1941). This original population was known to occur on Rock Island at the Falls of the Ohio River (Cronquist 1980), but has been extirpated by impoundment of the Ohio River (Evans 1987). The only known remaining populations of this species are from sites in and around Blue Licks Battlefield State Park, at the junction of Robertson, Nicholas, and Fleming Counties in north-central Kentucky (Figure 1A).

Solidago shortii occurs primarily in open, glade-like areas, often along the remnants of ancient buffalo (American bison) traces. The plants prefer open, sunny areas and do not compete well with other flowering plant species (Buchele et al. 1989). Invasion by non-native species, shading produced by woody taxa, and construction practices are among the major threats to the remaining plants. Recent surveys of the remaining sites identified 13 scattered populations of this species over an area of 12.2 km^2 (Buchele et al. 1989; Evans 1987; Figure 1A). It should be noted that population #13 is now extirpated, and population #6 has been reduced from a previous estimate of 2100 stems (Buchele et al. 1989) to less than 25 stems through intentional destruction by a resident landowner.

Prior investigations have focused on phenology and analysis

of life history. An exhaustive examination of autecological parameters included edaphic factors, light intensity, water relations, interspecific competition, and an overview of pollination ecology (Buchele et al. 1989, 1991, 1992a, 1992b). A subsequent series of studies focused on seed and seedling ecology, with evaluations of germination requirements, persistence of seeds in the seed soil bank, and effects of interspecific competition on seedlings (Walck et al. 1997a, 1997b, 1997c, 1997d, 1997e, 1998). Some general trends have emerged (e.g., the deleterious effect of interspecific competition on *Solidago shortii*). However, as is the case with many highly endemic species, a precise elucidation of the mechanism(s) responsible for the narrow endemism of *S. shortii* is not available (Buchele et al. 1992b; Walck et al. 1997a).

In the course of our field investigations into the population biology of *Solidago shortii*, we encountered a rather remarkable range of intra- and interpopulational morphological variation. Such variation had not been previously documented in the literature, and was not noted in several reports produced for state and federal agencies. In addition, we encountered some specimens of *S. shortii* that appeared to morphologically grade toward other *Solidago* congeners, initially creating considerable confusion and calling into question the exact nature of this species' delineation.

These observations brought two questions to mind. First, do the plants currently classified as Short's goldenrod at Blue Licks (BL) belong to that taxon as defined by the plants from the Falls of the Ohio (FO) type locality? Second, if the Blue Licks populations are indeed *Solidago shortii*, what level of intra- and interpopulational morphological variation exists in this highly restricted endemic, and how does this level of variability compare to congeners from the same geographic area?

We utilized morphometric analysis at both the inter- and intraspecific levels combined with whole-plant comparisons to address these questions. We compared herbarium specimens of *Solidago shortii* (BL and FO populations) with specimens of other members of the subsection *Triplinervae* (Torr. & A. Gray) A. Gray to obtain the macrocharacters most useful in defining *S. shortii*. To test the multivariate reality of *S. shortii* (as defined by whole-plant comparisons) we then compared the unit we believed to be *S. shortii* to one member of subsection *Triplinervae* [*S. canadensis* L. var. *scabra* (Willd.) Torr. & A. Gray] and to the two additional sympatric goldenrod species (*S. ulmifolia* Muhl. and *S.*

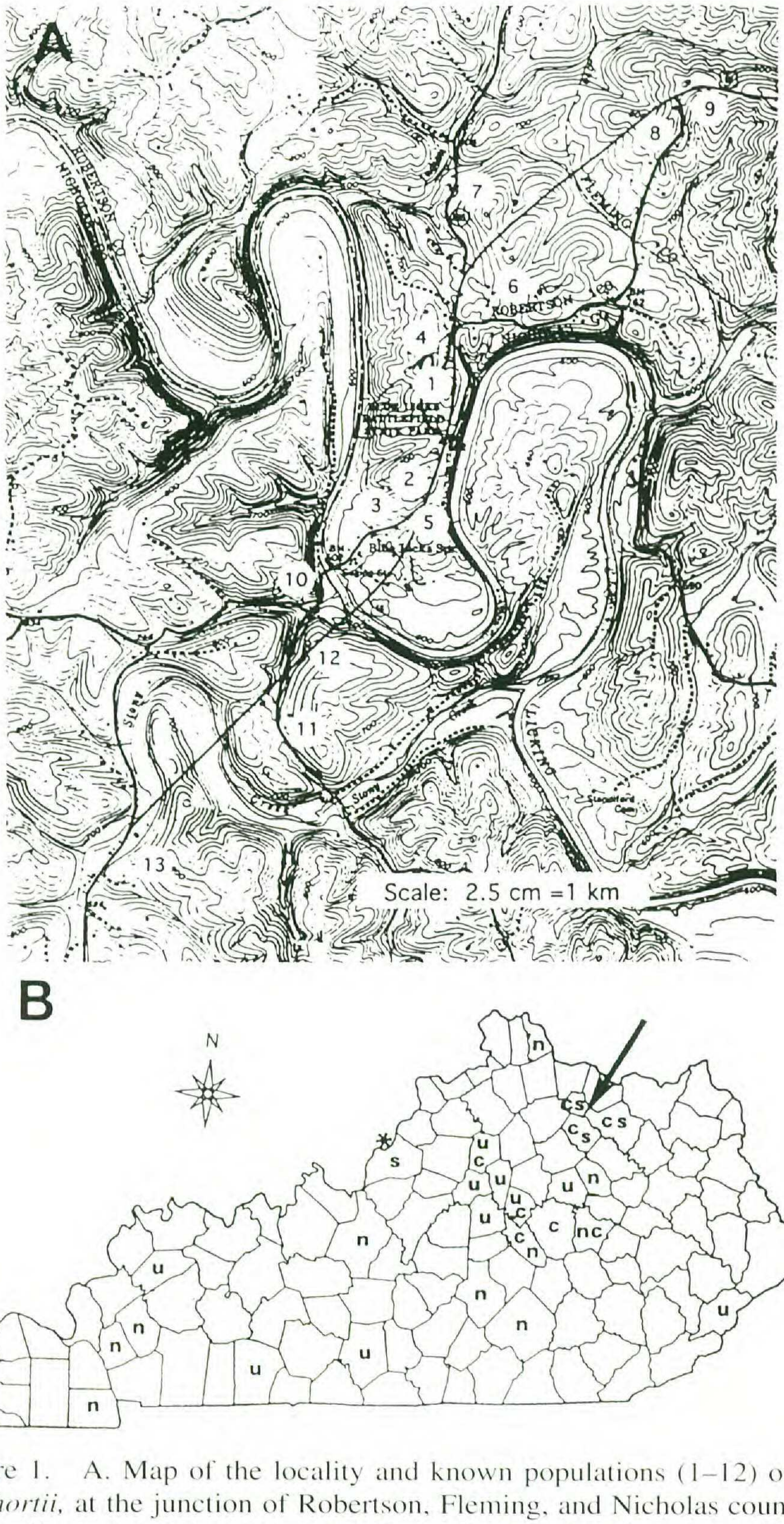

Figure 1. A. Map of the locality and known populations (1–12) of *Solidago shortii*, at the junction of Robertson, Fleming, and Nicholas counties in northern Kentucky. Populations #1, 7, 8, 9, 11, and 12 were sampled as described for morphometric analysis. The distribution map and numbering system is from Evans (1987). B. County map of Kentucky, showing the

nemoralis Aiton) using Principal Components Analysis (PCA) and Discriminate Function Analysis (DFA). In order to determine the range (quantitative limits) and distribution (intra- vs. inter-populational) of the variation, we undertook a second morphometric analysis of sampled individuals from different populations of *S. shortii* at BL, treating each population as a separate entity and determining the extent of the morphological variation relative to other *S. shortii* populations.

MATERIALS AND METHODS

Whole-plant comparisons. Eighty herbarium specimens annotated as *Solidago shortii* were examined, including 21 specimens from the FO type locality. These were compared to specimens of the five members of the subsection *Triplinervae* present in the eastern United States (*S. canadensis*, *S. gigantea* Aiton, *S. rupestris* Raf., *S. leavenworthii* Torr. & A. Gray, and *S. tortifolia* Elliott) and to the two remaining *Solidago* species present at Blue Licks (*S. ulmifolia* and *S. nemoralis*). Characters useful in whole-plant diagnoses of species membership were noted.

Morphometric analysis. An initial herbarium study of 44 specimens representing the four taxa (*Solidago shortii*, *S. nemoralis*, *S. canadensis* var. *scabra*, and *S. ulmifolia*) was conducted to define those character states that would be most useful for morphometric comparisons (county localities indicated in Figure 1B). Nineteen characters (Table 1; Figure 2) were considered. Fourteen *S. shortii* specimens were measured, including seven collected from the type locality in the mid-nineteenth century, and ten specimens each were measured for the remaining three taxa. Variation present within a single specimen was tested by dissecting five flowering heads per plant for the first three specimens of *S. ulmifolia*, *S. nemoralis*, and *S. canadensis*. One specimen of *S. shortii* was analyzed in this manner, with lower sample

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collection localities of herbarium specimens of *S. canadensis* var. *scabra* (c), *S. nemoralis* (n), *S. ulmifolia* (u), and *S. shortii* (s) sampled for the initial herbarium study. The extirpated population of *S. shortii* is designated by an asterisk. The arrow indicates the area enlarged in part A.

Table 1. List of morphological characters, with abbreviations, analyzed on field and/or herbarium samples of the four *Solidago* taxa and utilized for morphometric analyses. Sample size: *S. shortii* (68), *S. nemoralis* (25), *S. ulmifolia* (25), *S. canadensis* var. *scabra* (25).

Abbreviation	Morphological Character
Continuous Characters	
1. RTUB	Length of ray tube
2. RSTR	Length of ray strap
3. RWID	Width of ray strap
4. LWIP	Distance from widest portion of leaf to leaf apex
5. INVL	Height of involucre
6. PHYW	Width of middle series phyllary
7. DPAP	Length of disk pappus
8. RPAP	Length of ray pappus
9. DCOR	Length of disk corolla
10. LEAL	Length of cauline leaf from the upper plant portion
11. LEAW	Width of cauline leaf from the upper plant portion
12. STOT	Length of ray strap/total length of ray corolla
13. TTOT	Length of ray tube/total length of ray corolla
14. RCOR	Length of ray corolla
15. LWRT	Length of cauline leaf/width of cauline leaf
Discontinuous Characters	
16. INFP	Number of hairs present inside a 0.75 mm^2 stem area inside the inflorescence
17. UPPP	Number of hairs present inside a 0.75 mm^2 stem area on the upper portion of the plant
18. LEAP	Number of hairs present inside a 0.75 mm^2 area on the underside of a leaf in the upper plant portion
19. MDVP	Number of hairs present along a 0.5 mm^2 section of the midvein on the lower side of a leaf in the upper plant portion

size due to the limits of specimen availability for such sampling. Characters 5–15 (Table 1) were measured for each head, and the resulting means from each head were compared. This revealed little variation within a single plant, and subsequent analysis included only one head per plant.

The values obtained from this initial herbarium study were analyzed using PCA to identify the characters that exhibited the highest loadings. These informative characters were the focus of analysis in subsequent studies.

Field studies were conducted between September 5 and October 9, 1998. Three leaves and three flowering heads were taken from plants along linear transects in six of the twelve known

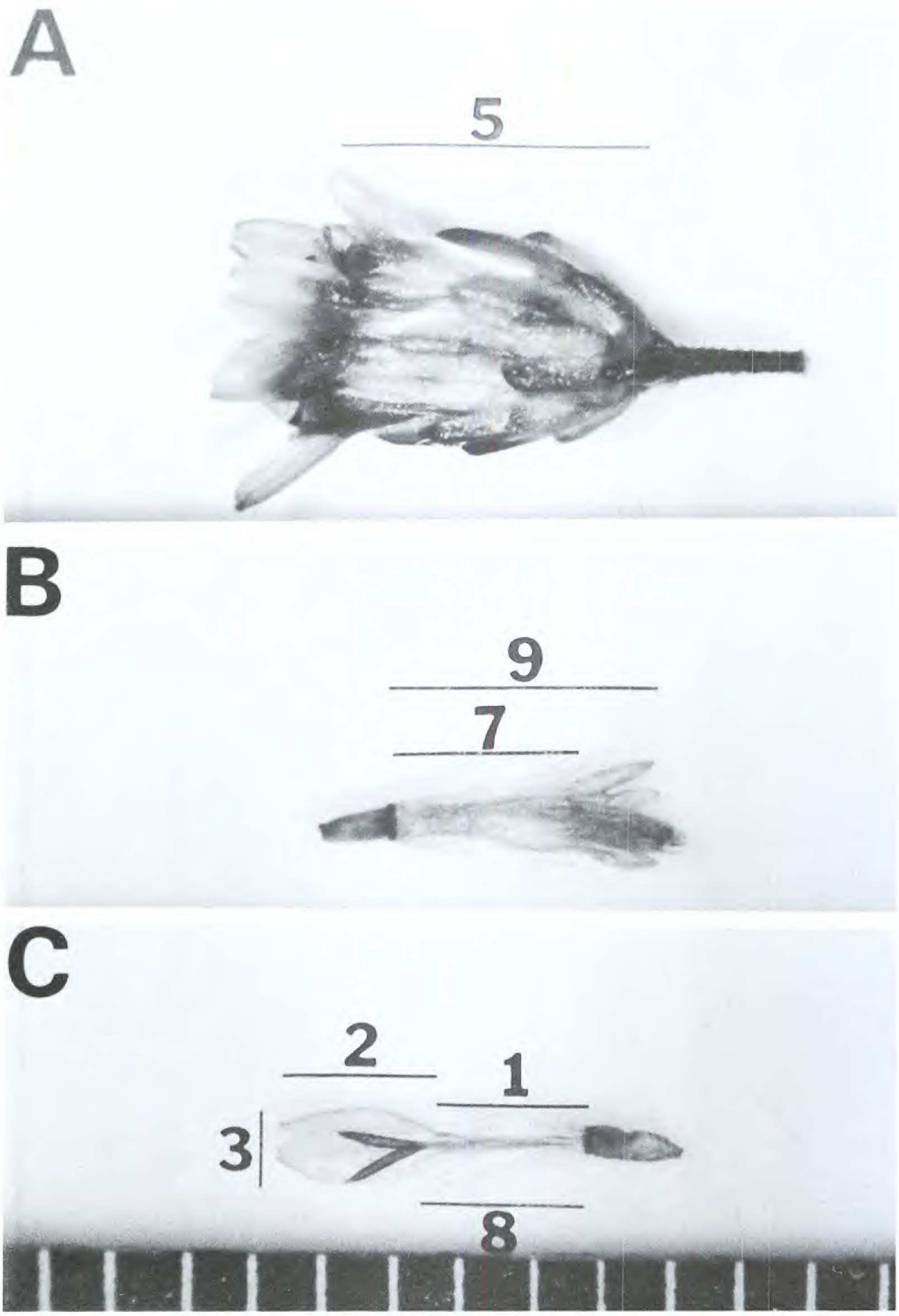

Figure 2. Selected floral characters utilized in the analysis. A. Flowering head of *Solidago shortii*. B. Disk floret. C. Ray (ligulate) floret. Divisions present on bottom bar are in mm. Numbers denoting characters correspond with those in Table 1.

populations (Figure 1A). *Solidago shortii* specimens were sampled from populations #1, 7, 8, 9, 11, and 12; *S. nemoralis* from #4 and 12; *S. ulmifolia* from #7 and 9; and *S. canadensis* var. *scabra* from #4, 9, and 11. Vegetative material was measured fresh, with floral material dried for later analysis. Floral material was re-hydrated in a detergent solution and measured with the aid of a dissecting scope equipped with an optic micrometer. To assess the possibility of alteration of features on herbarium specimens due to drying, fresh vegetative material was measured and subsequently vouchered. Ten specimens were examined one year after preparation, and LEAL (Table 2) was again measured from the dried specimens. Drying of leaf material did result in a small, consistent reduction in leaf length. Dried leaves were on average 97.52% (n = 10, SD = 0.96%) of their fresh length. Pertinent vegetative measurements from the FO herbarium specimens were adjusted to take into account this slight shrinkage. All floral material taken fresh from the study sites was dried according to standard herbarium practices before rehydrating and analysis; therefore comparisons with floral material from the herbarium sheets were made without numerical adjustment.

A total of 99 plants (54 *Solidago shortii*, 15 *S. nemoralis*, 15 *S. ulmifolia*, and 15 *S. canadensis* var. *scabra*) were analyzed in the fashion described above. To reduce the possibility of variation due to geographic factors or chromosomal races (Brammell and Semple 1990), individual plants of the latter three taxa were sampled from populations in Kentucky found in proximity or within the populations of *S. shortii*. Seven *S. shortii* herbarium specimens from the extirpated type locality were analyzed with the 54 *S. shortii* specimens sampled from the BL populations. Summary statistics for the 99 field specimens are presented in Table 2.

The data generated from the field study were analyzed with PCA and DFA. In each analysis, characters were excluded to eliminate pairs of characters that were likely genetically redundant (as revealed by high Pearson correlation coefficient values between all possible pairs of characters). The final character suites (along with component loadings) used in the PCA for each pairwise comparison are presented in Table 3. The characters used in DFA were LWIP, INVL, PHYW, RTUB, RSTR, STOT, and RPAP, with four of these (LWIP, RTUB, STOT, and RPAP) log-transformed because they were non-normal. To visualize the results of the PCA, the components exhibiting the highest loadings

Table 2. Means ± SD and ranges for morphological characters measured for the four *Solidago* taxa at Blue Licks. Character abbreviations are defined in Table 1. All measurements are in mm, except LEAL, LEAW, and LWIP, which are in cm. n = sample size. *n = 5 for LEAL, LEAW, LWIP.

Character	*S. shortii* (n = 54)	*S. nemoralis* (n = 15)	*S. ulmifolia* (n = 15)	*S. canadensis* var. *scabra* (n = 15)*
LEAL	2.0 ± 0.891 (0.44–4.38)	1.1 ± 0.345 (0.6–1.79)	4.4 ± 1.102 (2.44–6.94)	4.5 ± 0.740 (3.42–5.31)
LEAW	0.5 ± 0.962 (0.038–1.0)	0.3 ± 0.096 (0.17–0.52)	1.1 ± 0.349 (0.520–1.870)	0.7 ± 0.142 (0.50–0.89)
LWIP	1.0 ± 0.535 (0.089–2.6)	0.4 ± 0.152 (0.18–0.77)	2.3 ± 0.527 (1.41–3.35)	2.8 ± 0.590 (1.90–3.31)
INVL	4.6 ± 0.473 (3.6–5.5)	4.0 ± 0.279 (3.5–4.4)	3.5 ± 0.460 (3.0–4.3)	3.9 ± 0.493 (3.0–4.5)
PHYW	0.9 ± 0.109 (0.7–1.2)	0.7 ± 0.070 (0.6–0.8)	0.7 ± 0.108 (0.5–0.9)	0.5 ± 0.086 (0.4–0.7)
DCOR	3.6 ± 0.301 (2.9–4.4)	3.0 ± 0.262 (2.3–3.3)	2.7 ± 0.242 (2.1–3.0)	3.6 ± 0.304 (3.1–4.0)
RTUB	1.8 ± 0.261 (1.2–2.4)	1.8 ± 0.263 (1.4–2.3)	1.2 ± 0.158 (0.9–1.4)	2.1 ± 0.255 (1.8–2.7)
RSTR	2.1 ± 0.306 (1.5–3.0)	1.5 ± 0.216 (1.1–1.8)	1.5 ± 0.292 (1.1–2.1)	1.7 ± 0.379 (1.0–2.3)
STOT	0.552 ± 0.044 (0.455–0.688)	0.456 ± 0.027 (0.406–0.5)	0.561 ± 0.028 (0.520–0.618)	0.437 ± 0.055 (0.333–0.537)
RWID	0.9 ± 0.133 (0.6–1.2)	0.6 ± 0.070 (0.5–0.7)	0.7 ± 0.18 (0.4–1.1)	0.3 ± 0.106 (0.1–0.5)
RPAP	2.5 ± 0.286 (1.8–3.3)	2.2 ± 0.210 (1.8–2.6)	1.7 ± 0.240 (1.3–2.2)	2.7 ± 0.429 (1.9–3.6)

Table 3. Characters, with loadings for each principal component, used in comparisons of *Solidago* species pairs in Principal Components Analysis. Character abbreviations are defined in Table 1.

Species Comparison	Character	Component Loading (1)	Component Loading (2)
S. shortii/*S. nemoralis*	LWIP	0.483	–0.414
	INVL	0.782	0.293
	RTUB	0.013	0.891
	RSTR	0.896	0.122
	STOT	0.762	–0.552
	RWID	0.712	0.017
	RPAP	0.726	0.357
S. shortii/*S. canadensis* var. *scabra*	INVL	0.754	0.286
	DCOR	0.398	0.848
	RTUB	–0.392	0.869
	RSTR	0.864	0.327
	STOT	0.877	–0.368
	RWID	0.822	–0.210
S. shortii/*S. ulmifolia*	LWIP	–0.667	0.626
	PHYW	0.770	–0.001
	RTUB	0.846	–0.053
	RSTR	0.807	0.051
	RWID	0.645	0.655

were plotted against each other in a graphical manner (Figures 3–5). For the DFA, factors 1 and 2 were plotted against each other in the same fashion (Figure 6). All statistical analyses of data were performed using SYSTAT version 5.2 (1992, SPSS Inc., Evanston, IL) on an Apple Power Macintosh computer containing a G3 processor.

RESULTS

Species circumscription. Plants with paniculate inflorescences; tri-nerved, glabrous leaves; fewer than 8 ray florets; and involucres greater than 3.5 mm in length formed a clear morphological unit that encompassed the range of variation present in both the BL and FO *Solidago shortii* specimens. Whole-plant comparisons also revealed the characters most useful in pairwise comparisons between *S. shortii* and each of the other species examined. *Solidago shortii* had fewer (5–7 vs. 8–13) and broader

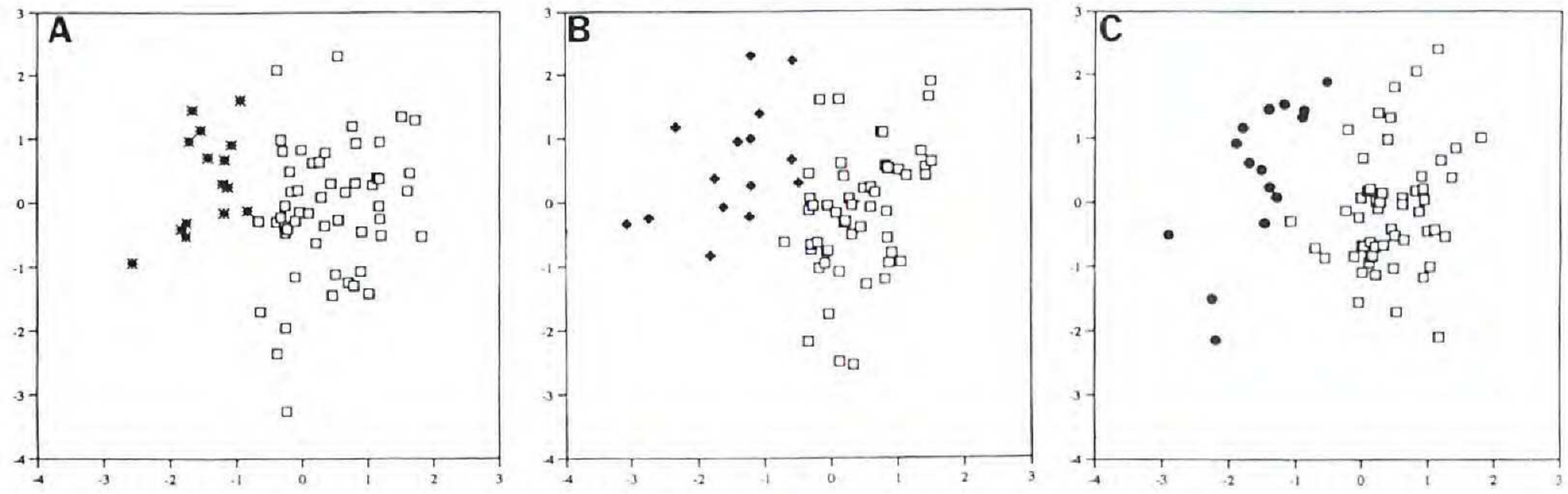

Figure 3. Scattergrams showing results of Principal Components Analysis for interspecific comparisons. Panels A, B, and C show pairwise comparisons between individual plants of *Solidago shortii* from the Blue Licks population (rectangles) and individuals of *S. nemoralis* (stars), *S. canadensis* (diamonds), and *S. ulmifolia* (circles), respectively. Factor 1 is plotted along the abscissa, Factor 2 along the ordinate.

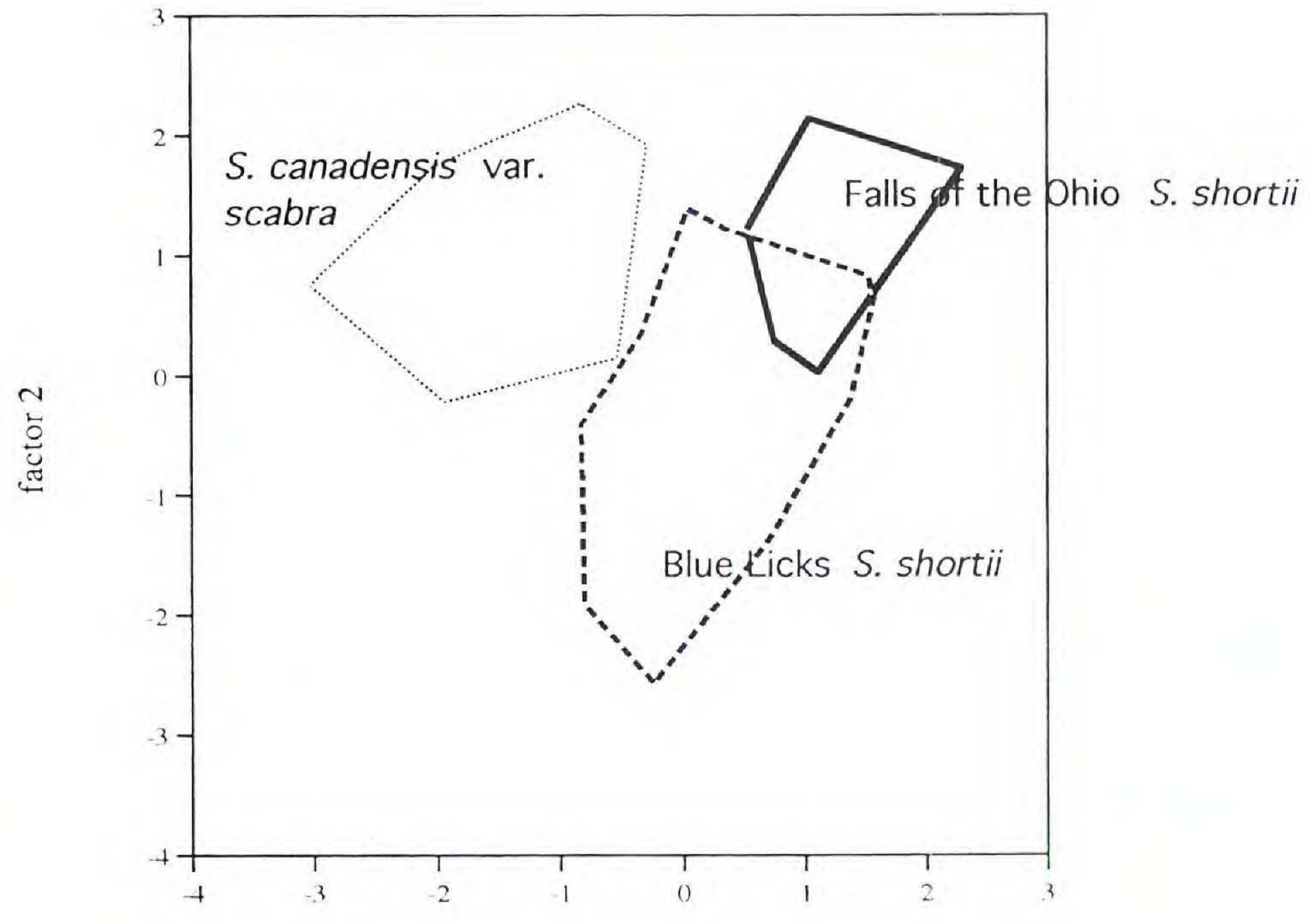

Figure 4. Scattergram showing results of the Principal Components Analysis of *Solidago shortii* in comparison with *S. canadensis* var. *scabra*. The species' polygons are demarcated by individual specimens of each respective taxon sampled herein; for clarity, the individual specimens have been omitted from the figure. The extant Blue Licks and extirpated Falls of the Ohio populations of *S. shortii* are indicated by their respective polygons.

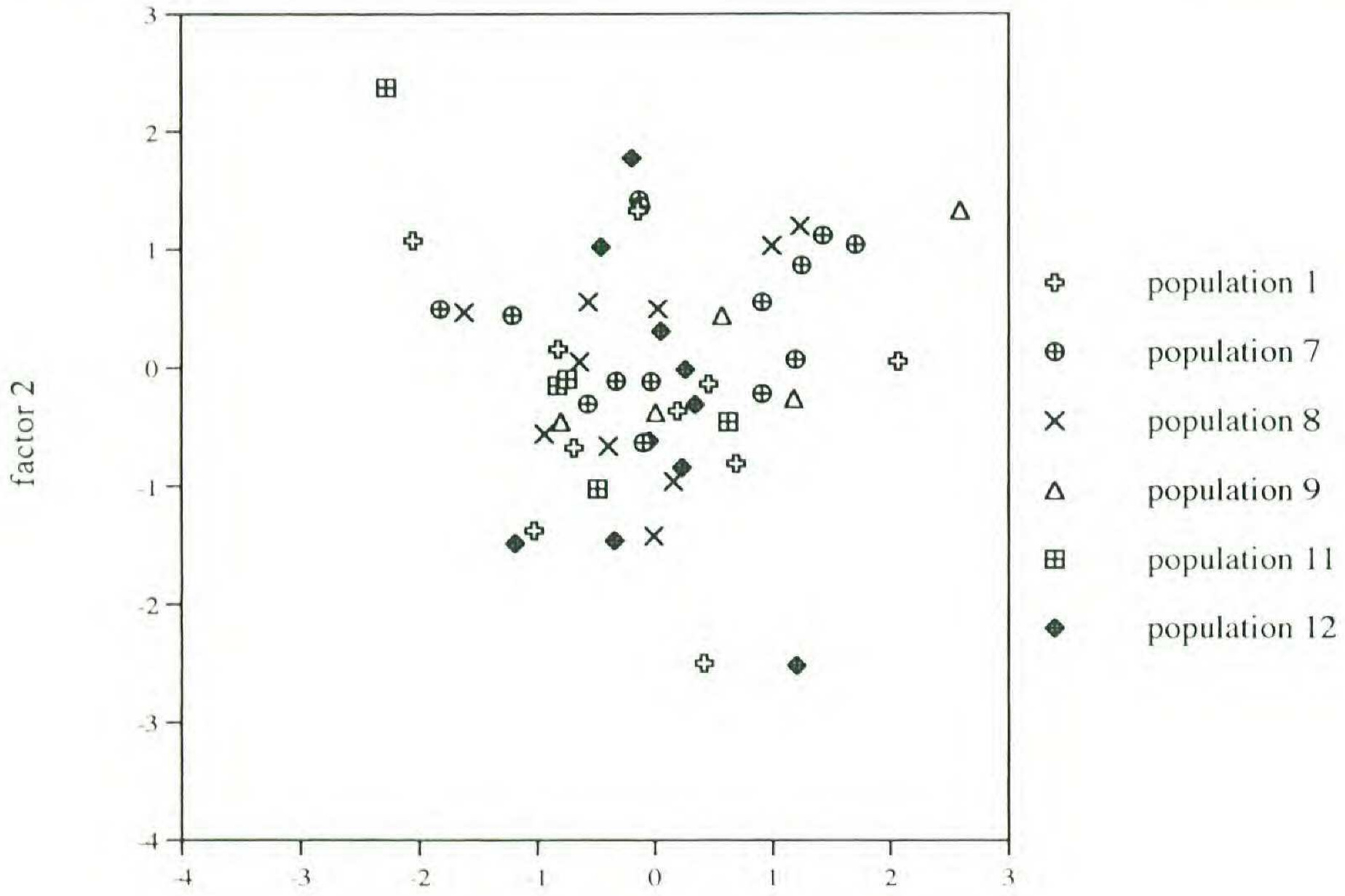

Figure 5. Interpopulational variation present within *Solidago shortii* from Blue Licks and vicinity, Kentucky. Each set of identical symbols represents individuals from a single population; in all, six populations are shown.

(0.6–1.2 vs. 0.1–0.5 mm) ray florets relative to *S. canadensis* var. *scabra*. *Solidago shortii* also exhibited glabrous leaves, while the leaves of *S. canadensis* var. *scabra* were densely pubescent. Short's goldenrod exhibited fewer (5–7) rays relative to *S. leavenworthii* (10–16). *Solidago shortii* had fewer (5–7 vs. 7–15) ray florets than *S. gigantea*, and the sub-inflorescence stem of *S. shortii* was pubescent, compared to the glabrous sub-inflorescence stem of *S. gigantea*. Short's goldenrod had a longer involucre (3.6–5.5 vs. 2.5–4.0 mm) relative to *S. tortifolia*. The width of the largest leaves of *S. shortii* (> 1.0 cm) were also diagnostic relative to those of *S. tortifolia* (< 1.0 cm). *Solidago shortii* had a longer involucre (3.6–5.5 mm) than *S. rupestris* (2.0–3.1 mm). Pubescence characters best differentiated *S. shortii* from *S. ulmifolia*. *Solidago shortii* had a pubescent sub-inflorescence stem and glabrous abaxial leaf midveins, relative to the glabrous sub-inflorescence stems and pilose abaxial leaf midveins of *S. ulmifolia*. *Solidago shortii* had wider (0.6–1.2 vs. 0.5–0.7 mm) ray florets relative to *S. nemoralis*. The glabrous leaves of Short's

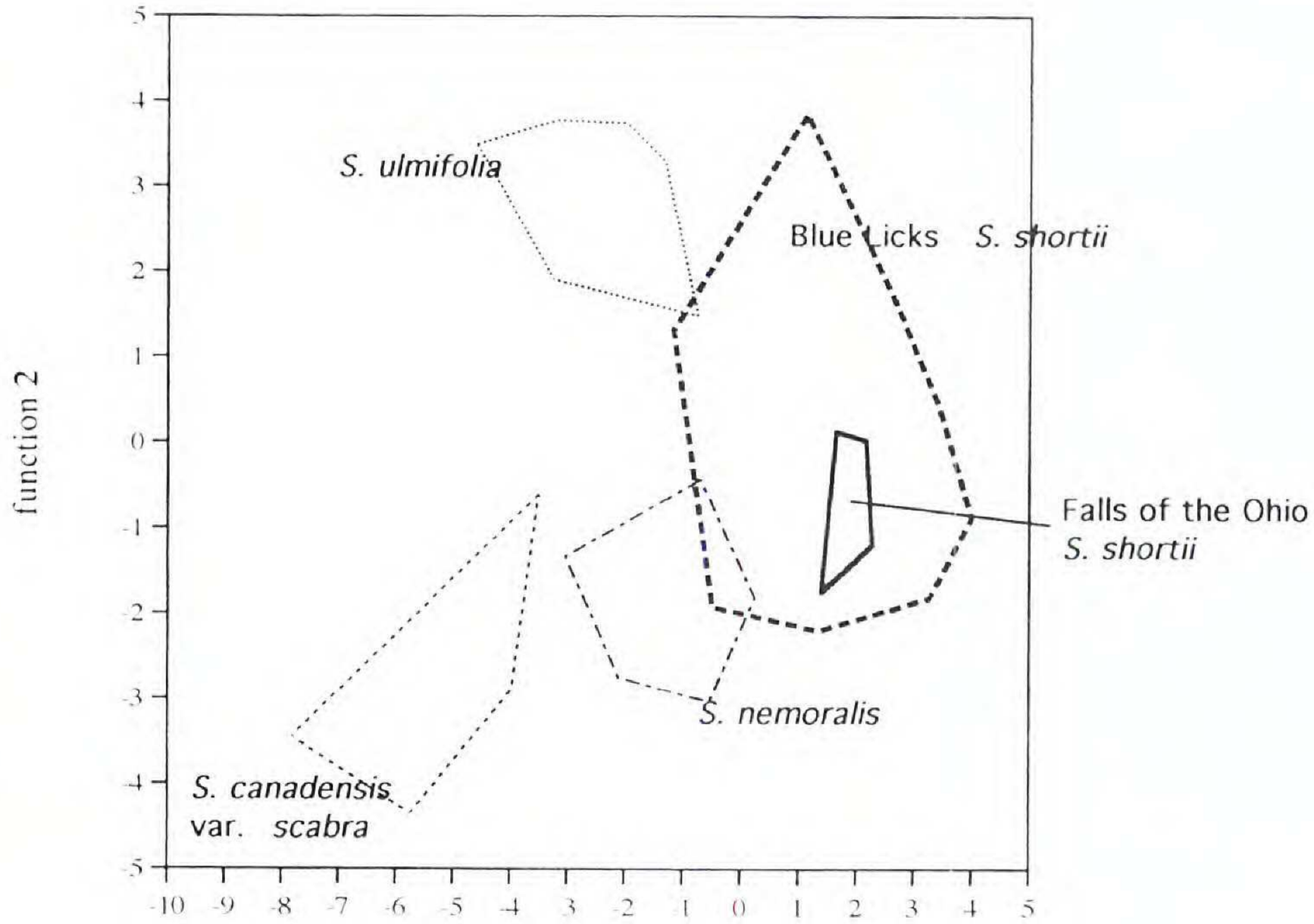

Figure 6. Scattergram representing the Discriminate Function Analysis of all species considered in the morphometric analysis. The species' polygons are demarcated by individual specimens of each respective taxon sampled herein; for clarity, the individual specimens have been omitted from the figure. The extant Blue Licks and vicinity, and extirpated Falls of the Ohio populations of *Solidago shortii* are indicated by their respective polygons.

goldenrod also helped distinguish it from *S. nemoralis*, which exhibited densely puberulent leaves.

All *Solidago shortii* specimens from the BL populations were grouped with the FO specimens using these criteria. In addition, the first plants taken from the Blue Licks area in 1939 were annotated as *S. shortii* by M. L. Fernald and others following review alongside the original FO material archived at the Gray Herbarium (Braun 1941). The morphometric analysis also supported the idea that the BL and FO specimens belong to the same taxon. The BL and FO *S. shortii* specimens, in pairwise comparisons with *S. canadensis* var. *scabra*, *S. nemoralis*, and *S. ulmifolia*, consistently formed a distinct cluster segregate from those clusters formed by the other taxa (Figure 3A–C). Furthermore, when viewed as distinct clusters, the specimens of Short's goldenrod from the Falls of the Ohio and from Blue Licks formed two overlapping clusters that segregated from *S. canadensis* var. *sca-*

bra (Figure 4), a close phylogenetic relative in subsect. *Triplinervae* (Semple et al. 1999). The DFA also provided evidence of the unity of the BL and FO specimens. When treated as separate *a priori* groups, the cluster formed by the FO specimens was completely imbedded within the BL cluster (Figure 6). In addition, 4 of the 54 BL *S. shortii* specimens were misclassified as belonging to the FO *a priori* group.

Species variation. Of interest were the relative amounts of morphological variation present at the Blue Licks study sites in three common *Solidago* species compared to *S. shortii*. Short's goldenrod is known only from the aforementioned sites, therefore our sample area was restricted to them. The common *Solidago* species exhibit cytological and/or geographic races throughout their range of occurrence (Brammell and Semple 1990; Cronquist 1980). Sampling only from the Blue Licks sites excluded the morphological variation which results.

The scales on the PCA graph axes (Figures 3–5) are relative. Therefore, comparisons within and among the graphs can be made. In these graphs the area occupied by a group of sampled individuals of the same species was directly related to the amount of measured morphologic variability. *Solidago shortii* occupied a considerably larger area than *S. nemoralis* and an area comparable to that of *S. canadensis* var. *scabra*, reflecting an equal or greater degree of morphologic variability relative to these two taxa (Figure 3A, B). The area occupied by *S. ulmifolia* was slightly larger than that occupied by *S. shortii* (Figure 3C), indicating that the sampled specimens of S. *ulmifolia* exhibited a slightly higher degree of morphologic variability. Of some concern were the relatively small sample sizes (15 each) present for the three common species. In order to investigate the effects of sample size, data sets were formed using the 15 samples of each of the common species (*S. canadensis* var. *scabra*, *S. nemoralis*, and S. *ulmifolia*) combined with 15 *S. shortii* samples taken from identical populations as the common species. These two data sets were analyzed in the same manner as the large sets, and similar variational ranges were observed (data available upon request from J.B.B.). The rare *S. shortii* exhibited a comparable or greater extent of phenotypic variability than two of the three common species to which it was compared from the BL study area.

Population variation. The level of intra- and interpopulational variation within *Solidago shortii* from Blue Licks was significant. Although all of the sampled BL populations overlapped, several of the populations (#1, 9, 11, and 12) contained individual specimens that were extreme outliers (Figure 5).

DISCUSSION

Solidago shortii was first collected by Dr. C. W. Short from Rock Island at the Falls of the Ohio River, Louisville, Kentucky, in 1840 (Beck et al. 1999). This site was destroyed by inundation upon the construction of the McAlpine Locks and Dam in the 1920s (Baskin et al. 1986). The occurrence of the species at the Blue Licks locality was reported by Braun (1941), and is the only known occurrence of the species (Buchele et al. 1989; Evans 1987). One possible reason for the limited distribution of this species is its possible dependence on disturbance by migrating eastern woodland American bison (Braun 1941). Upon extirpation of the bison, Short's goldenrod may have experienced a concomitant decline, due perhaps to increased competition from both native and invasive plant species (Buchele et al. 1989).

Whole-plant comparisons with both closely related and sympatric goldenrod species indicate that *Solidago shortii* is a distinct taxon, and morphometric comparisons between *S. shortii* and a subset of these species provides supporting evidence. These two approaches provide even stronger evidence to support the taxonomic contention that the BL populations are indeed *S. shortii* as described from the FO material. Though the results of both PCA and DFA indicate that plants from BL and FO are taxonomically identical, the placement of specimens of *S. shortii* from these two locations differ in the two analyses. The FO specimens are completely embedded in the cluster of BL specimens in the DFA plot (Figure 6). On the PCA plot, however, FO specimens appear at the end of the BL cluster and only partially overlap the BL specimens (Figure 4). Two factors account for the discrepancy between the DFA and PCA results. First, different characters were included in DFA and PCA, since different taxa were included in these analyses. Second, more taxa were included in the DFA than the PCA. The inclusion of more taxa in a DFA or PCA requires the simultaneous analysis of more sets of diagnostic characters, with the resultant diminishment of resolution between adjacent

specimen clusters. Thus, the FO specimens appear more different from the BL specimens on the PCA plot than they do on the DFA plot because, on the PCA, FO and BL are being compared with only one other *Solidago* taxon (vs. three other taxa on the DFA plot). Differences do exist, however, between the BL and FO specimens of *S. shortii*. Plants from FO tended to have larger leaves and capitular structures (disk corollas, ray pappus bristles, and involucres) than BL plants. Relative to the characters that distinguish *S. shortii* from other *Solidago* species, these differences between BL and FO plants are slight and do not justify treating FO as a different taxon than BL.

The morphological distinction could be due to spatial or temporal factors, or both. Temporal factors would likely entail subsequent genetic and morphological divergence over time between specimens collected from 1839–1842 from the Falls of the Ohio River and specimens collected at Blue Licks from 1939–present. Spatial factors would involve past restricted gene flow due to geographic distance (approximately 160 km) between the two localities. Another intriguing possibility is that of past differential gene flow to the separate populations of *Solidago shortii* (FO and BL) from taxa with close phylogenetic affinity (Nesom, pers. comm.). *Solidago shortii* is placed in subsection *Triplinervae* with three other species found in Kentucky—*S. canadensis* var. *scabra*, *S. gigantea*, and *S. rupestris*—and with two species from the southeastern U.S. (*S. leavenworthii* and *S. tortifolia*; Nesom 1993). Although only *S. canadensis* var. *scabra* is presently found within proximity of *S. shortii*, it is possible that in the post-Pleistocene landscape one or more of the above taxa might have been in close proximity to *S. shortii* at either FO or BL, and gene flow events could have contributed to the phenotypic variation seen between these populations. Given the dynamic nature of the vegetational changes in the post-Pleistocene environment of Kentucky and the eastern U.S. (Whitehead 1973; Wilkins et al. 1991; Wright 1976), it is plausible that distributional shifts in vegetation types and species allowed, at some point in time, for sympatric gene flow between sister taxa and *S. shortii*. The testing of this hypothesis would require the development of suitable molecular markers to allow for the dissection of the genome of *S. shortii* to determine if elements of other *Solidago* spp. genomes are present within Short's goldenrod.

The highly variable phenotype of this endemic species was first

observed among the initial collections of the plant by Dr. C. W. Short in 1839. Asa Gray, the species author of *Solidago shortii*, made note of morphological variation within the species in his original circumscription of the taxon from specimens obtained from Short. He noted two "varieties," designated β and γ, that differed from "typical" *S. shortii* specimens. However, he felt the extent or constancy of this variation was insufficient to warrant the formal designation of these entities as discrete taxa. It is remarkable that Gray noted this variation in a sample size of less than 10 specimens, from material collected at or near the Falls of the Ohio locality (Beck et al. 1999). Gray's observations do provide an independent qualitative assessment of the morphological variability found within the species.

A prevailing paradigm of rare and endangered species is that they often exhibit markedly decreased levels of phenotypic variability, as evidenced by limited ecological tolerances, homogeneous morphology, or genetic homozygosity. This study has shown a remarkable level of phenotypic variability in a species known from a single locality presently represented by perhaps several thousand individual plants.

There are four explanations that could account for the morphological variability found within Short's goldenrod. First, the variability could be due to epigenetic phenotypic plasticity, caused by external environmental influences. Among these could be edaphic factors, water relations, relative incipient solar radiation, and topographic influences (Tilman 1982, 1988). An exhaustive analysis by Buchele et al. (1989) revealed no striking differences among the habitats from which plants were sampled for this study.

The second possibility is that the inter- and intrapopulational differences have a genetic basis, and are due to the presence of different allelic and genic combinations within different individuals and populations. If gene flow between populations is restricted or nonrandom, then specific genetic differences could be established and maintained. Furthermore, if clonal reproduction is predominant over sexual reproduction, as has been suggested (Buchele et al. 1989), then the lack of meiotic recombination would maintain specific phenotypes over time. One would expect with the small numbers of individuals seen in some populations of *Solidago shortii*, that genetic drift would lead to a reduction of variation (Hastings 1997) within the smaller populations (e.g.,

#8, 11, 12). However, these three populations, whose numbers of stems ranged from 7-fold to 24-fold less than those of population #1, all showed a similar extent of variability. It should be noted that, due to the clonal nature of reproduction of *Solidago*, the number of stems noted above is not an indication of the number of plants, and we are assuming a direct correlation between the number of individual ramets in the population and the number of specific genets.

A third possibility is the production of hybrid offspring between *Solidago shortii* and one or more of the congener taxa at Blue Licks, due to cross-pollination. Interspecific hybridization has been suggested to occur in the genus (Cronquist 1980; Fernald 1970) and between members of different sections (Nesom 1993). There is, however, no direct experimental evidence that supports this possibility. The perceived gradation of the Blue Licks *S. shortii* plants toward the other *Solidago* taxa is thus interpreted as infraspecific variation. We have not been able to designate any specimens as being of hybrid origin through our statistical analyses. Two of the major insect associates of *S. shortii* flowers are the goldenrod soldier beetle (*Cauliognathus pennsylvanicus*) and the black blister beetle (*Epicauta pennsylvanica*; Buchele et al. 1992b). The soldier beetle exhibits a low frequency of movement between neighboring plants, which probably reduces the efficacy of cross-pollination and gene flow between adjacent individuals. The blister beetle is a flower predator, which could also reduce the readiness of pollinators to visit flowers harboring the beetle (Gross and Werner 1983).

The fourth possibility is that the level of variability we observed in *Solidago shortii* relative to the more common species is simply an artifact of the suite of characters we chose. Further studies should include either an expanded set of morphological characters, or the use of suitable molecular markers.

At present we lack evidence that provides unequivocal support for any of the four possibilities described above. However, our analyses do indicate that the sampled populations of *Solidago shortii* do not represent a homogeneous cluster, but rather an amalgam of different phenotypes.

The findings described here have implications for management of *Solidago shortii*. Given the level of morphological variability among populations, a rigorous genetic profile needs to be obtained from individuals of different populations at Blue Licks. If

the morphologic variability is mirrored at the genetic level, then each population could possess a profile distinct from other populations. Efforts at reintroduction of the species into former localities (i.e., the Falls of the Ohio River) or introduction into new habitats (perhaps along remnants of former bison traces) would need to take into account the nature of the variability, and the suitability of specific populations as sources of transplant material.

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